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A simple wheat germ diet for studying the nutrient requirements of the Indian meal moth, *Plodia interpunctella* (Hübner)☆

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Abstract

Indian meal moth infestation of processed cereal products during storage could be managed with little or no use of conventional pesticides if there was a greater recognition and use of the moth's innate vulnerabilities. Slowing the growth rate of the infesting larvae is a simple strategy that can decrease the amount of damage and decrease the frequency of pesticide intervention. The growth rates of Indian meal moths on different cereal products varies widely indicating product-related differences in nutrient availability for the insects. Nutrient availability depends upon both the amounts of nutrients available in the cereal product and upon physical characteristics of the product that restrict the assimilation of nutrients.

The development of control strategies for protecting processed cereal products based upon nutrient availability requires a simple, palatable test diet of known composition. Wheat germ mixed with 30% glycerol (w/w) provides a suitable growth medium for the Indian meal moth whose nutrients have been largely identified and quantified. Our studies indicate that dietary glycerol augments Indian meal moth

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growth and development on wheat germ by moisturizing the diet and probably provides a source of carbon and energy for larval growth.

Keywords: Stored-product moth; Indian meal moth; Moth nutrition; Cereal nutrients; Oligidic diet; Larval growth; Wheat germ; Glycerol

1. Introduction

Managing insect populations that infest stored commodities is a greater challenge today than previously because pesticide usage has become more restricted. The search for environmentally safe alternatives is the focus of research in many laboratories around the world. In our laboratory, we are seeking new approaches based upon the insect's behavior and physiology. When looking at the growth of the Indian meal moth on different processed cereal products the insect's growth rate was largely dependent upon the cereal providing the nutrients. Even though the products we examined were considered nutritious as part of a more complex human diet, they were not equally nutritious when serving as the sole nutrient source in the insect diet.

Moth populations infesting stored commodities might be managed by altering nutritive and physical characteristics of a processed commodity that would limit the availability of nutrients to the moth without compromising its nutritional value in the human diet. Preventing insect growth would be the most desirable outcome, but even decreasing the growth rate might be effective if it reduced the severity of the infestation and the frequency with which pesticide intervention was needed.

When seeking alternatives to conventional pesticides, the physical characteristics of the commodities need to be considered. For example, Indian meal moths and other flour moths, infest only the broken or damaged grain kernels because the larvae are unable to chew through the pericarp on the intact dry kernel (Locatelli and Limonta, 1998). We have noted that even the sugar coating on some breakfast cereals is too hard for newly hatched Indian meal moth larvae to penetrate (unpublished observations). Thus, the physical characteristics of a commodity can be an effective deterrent to moth infestation by limiting the availability of nutrients for larval growth.

However, in most processed commodities the integrity of the pericarp is removed either by crushing or grinding the grain, which exposes the endosperm and germ to the moth larvae. Mediterranean flour moths can utilize both the starch stored in the endosperm and other nutrients located in the germ for growth (Fraenkel and Blewett, 1946a). On the other hand, Indian meal moths and most other flour moth species utilize only the nutrients located in the grain's germ and bran (Madrid and Sinha, 1982) and are restricted to those cereal products that include one or both of these components (Fraenkel and Blewett, 1946a; Locatelli and Limonta, 1998). For our studies on the nutrient requirements of the Indian meal moth during commodity infestation, we needed a nutritionally complete, test diet of known nutrient composition that was a natural product where nutrient acquisition was unimpeded by physical factors. The oligidic diet described by Silhacek and Miller (1972) provided optimum nutrition for the growth and development of Indian meal moths but was too complex for studies investigating the moth's nutritional requirements. The wheat bran diet described by Finney and Brinkman (1967) and used by Johnson et al. (1992) was better suited, but was not ideal for this study. Fraenkel and Blewett (1943, 1946a, b) and Morère (1971a, b) described the nutritional requirements of the Indian meal moth and two related cereal moth species. Morère (1970) described a meridic diet for the Indian meal moth and also studied their nutritional requirements (Morère, 1971a, b, 1973, 1974). In this paper, we describe a relatively simple wheat germ diet which supports the growth and development of Indian meal moths in a fashion indistinguishable from that on the diet described by Silhacek and Miller (1972). Many, if not all, of the nutrients in wheat germ have been identified and quantified (US Department of Agriculture Nutrient Database, NDB No. 08084, 2002) which significantly contributes to any investigation on the nutrient requirements of the Indian meal moth.

2. Materials and methods

2.1. Test insects

Indian meal moths were reared at 30 °C, 70% relative humidity (r.h.) in clear polystyrene rearing boxes (14 cm × 19 cm × 9 cm deep) on the standardized *Plodia* diet described by Silhacek and Miller (1972), consisting of ground dog food, rolled oats, cornmeal, whole wheat flour, wheat germ, brewer's yeast, glycerol, and honey. A 16:8 h (L:D) photoperiod was maintained except that the scotophase was routinely initiated at 12:00 p.m. Twenty-one days after culture setup, moths were very briefly anesthetized with CO_2 and transferred during the 4-h period preceding the scotophase from rearing boxes into an oviposition chamber for egg laying. For culture and experimental setups, eggs were collected at incubation conditions over a 1-h interval and placed on diet before the end of the 4-h period.

2.2. Assessing the attractive and nutritive components of commodity infestation

The infestation of a cereal product relies upon its attraction of female moths to lay eggs and its ability to support the growth of the newly hatched larvae. To assess these two infestation components we developed an assay using one half (9.1 m × 1.85 m × 2.4 m high) of a model warehouse maintained at 30 °C, 70% r.h. and 16:8 h (L:D) photoperiod (Silhacek et al., 2003). For each test, 50 g portions of five products [*Plodia* rearing diet, Kretschmer wheat germ, Ol' Roy dog food (Dinner Rounds), whole wheat flour, and Kellogg's corn flakes] were measured into paper cups (Sweetheart food cup, VS512). Two open cups of each product were placed on each of three pallets evenly spaced along the length of the test area. About an hour before a scotophase, ca. 1500 carefully aged pupae ($6\frac{1}{2} \pm \frac{1}{2}-$ d-old) were also placed in the test area as described by Silhacek et al. (2003). Moth emergence began 6 h before the next scotophase and was largely complete when the lights went out 6 h later. Mating and oviposition occurred during the remaining 32 h of the 56 h test period. This test period was selected to prevent infestation of the cereal products in the cups by larvae hatching from eggs laid outside the cups. Silhacek and Miller (1972) reported that Indian meal moth eggs hatch after 62 h when incubated at 30 °C.

One series of product cups, consisting of one cup of each cereal product from each pallet, were closed with a lid at the end of the test period and incubated for 10 d in the rearing incubator. The other series of product cups were handled similarly to the first series except that 30 g of *Plodia* diet was added before closing the cups with a lid. The number of larvae that developed in the test cups, when *Plodia* diet was added, provided a measure of the products attractiveness. Comparing these numbers with those in cups without *Plodia* diet added indicated which products had nutritional limitations that restricted the level of infestation.

In each assay, the series of cups containing *Plodia* diet was used as the internal standard for both, attraction and nutritional quality. Each experiment was repeated three times to obtain the infestation levels reported here. We used analysis of variance to analyze the data (PROC GLM, SAS Institute, 2001).

2.3. Measuring larval growth

The growth of Indian meal moths on the five cereal products used in this study was assessed by comparing the larval growth curves. One product, wheat germ, was examined more extensively to determine if growth could be improved by adding glycerol. Five wheat germ/glycerol diets were prepared by supplementing Kretschmer's wheat germ with 0%, 10%, 2%, 30%, and 40% glycerol (w/w). In some experiments where glucose was substituted for a portion of the glycerol, the sum of glycerol plus glucose contributed 40% of the final diet weight.

Larval growth on the different cereal products and the various wheat germ test diets were obtained by placing 25 freshly laid (0–1-h-old) eggs on 10-g portions of the test diet in 30-dram polystyrene vials with a screw cap bottom and a screened (0.150 mm aperture, 2.5 cm diameter) top. After incubating at rearing conditions for 10 d, a group of five larvae were randomly selected from each container of test diet, weighed, and then returned to the diet container for continued incubation. At 10 d the control larvae weighed 2–3 mg; because smaller larvae were more fragile, slow growers were not weighed until they attained the same size as the 2–3 mg control larvae. Successive groups of five larvae were randomly selected daily from each test diet container and weighed as the larvae grew to maturity. Each experiment consisted of three diet containers for each commodity. Three experiments were averaged to construct the growth curves presented here.

We used non-linear regression (PROC NLIN, SAS Institute, 2001) to fit a logistic growth curve to describe changes in weight of the larvae over time. The equation is $\text{weight} = a/(1 + e^{(-(\text{day}-b)/c)})$, where a is the predicted maximum weight, b is the day at which half of the maximum growth is attained, and c is the number of days it takes to go from $\frac{1}{2}$ to $\frac{3}{4}$ of the maximum growth. We used a multivariate analysis of variance to test for differences in a, b, and c simultaneously (PROC GLM, SAS Institute, 2001).

3. Results and discussion

3.1. Distinguishing attraction from nutrition

Five different cereal products were placed in a model warehouse along with 1500 carefully aged pupae as described by Silhacek et al. (2003). The newly emerged Indian meal moth adults sought out and oviposited on the cereal products that attracted them. The levels of infestation differed among the five products. These differences could be attributed to either, differences in the attractiveness of the cereals to ovipositing moths or differences in the nutritional content of the

Table 1
Indian meal moth infestation of different commodities by direct oviposition during storage in a model warehouse; the addition of *Plodia* diet after oviposition distinguished nutrition from attraction

Commodity	Number of infesting larvae/cup[a]	
	With *Plodia* diet	Without *Plodia* diet
Plodia diet	252 ± 37	269 ± 60
Wheat germ	134 ± 12	140 ± 16
Whole wheat flour	126 ± 29	128 ± 40
Dog food	61 ± 16	43 ± 10
Corn flakes	48 ± 18	0

[a]Each value is the average number of larvae/cup ± SEM, replicated three times in each of three experiments. ANOVA results—Commodity: $F = 14.4$; df = 3, 16; $P < 0.01$. Presence or absence of *Plodia* diet: $F = 0.01$; df = 1, 16; $P = 0.94$. Interaction: $F = 0.10$; df = 3, 16; $P = 0.96$. Corn flakes were excluded from the analysis because there was no variation in number of larvae when no supplemental *Plodia* diet was provided, so means were not homogeneous and could not be homogenized when corn flakes were included.

cereal products that would support the growth of developing larvae. Both of these parameters were assessed as described in Methods for the five cereal products that were of interest in this study and which exemplified the range of the Indian meal moth responses (Table 1).

The relative attractiveness of the different cereal products to ovipositing females was quantified by determining the level of infestation in product cups when *Plodia* diet was added after the 56 h test period. The results (Table 1) showed that wheat germ was more attractive to Indian meal moths than dog food or corn flakes. All were less attractive than the standard *Plodia* diet.

The nutritional quality of the cereal products was assessed in the same experiments by counting the numbers of infesting larvae in the test cups of each cereal product when no *Plodia* diet was added. Four of the five cereals yielded similar numbers of larvae whether or not *Plodia* diet was added to the cups at 56 h, indicating that nutrition was not a factor contributing to the level of infestation. However, no larvae were found in Kellogg's corn flakes unless *Plodia* diet was added to the cereal at 56 h. This observation indicated that corn flakes did not provide the nutrients required for the development of newly hatched Indian meal moth larvae. We did not determine whether this was the result of a nutritive or physical characteristic of corn flakes. However, these observations with corn flakes support the hypothesis that cereal products, ideal for storage, could be designed to not support the development of an infesting moth population on the one hand, but still provide an acceptable nutrient source for domestic consumption on the other.

3.2. Growth rates

The level of infestation achieved during the storage of a cereal product is directly related to the rate that moths grow and develop on that product. If the growth and development of an infesting moth population on a particular product is slow, the level of infestation may not become significant during a short storage period. Protecting such a product during longer periods of storage may require the application of conventional control methods, but at less frequent intervals when compared to other commodities that support strong larval growth. Thus, the slowing of insect growth by nutritional or environmental adjustments would be a useful adjunct in managing pest insect populations that would limit the introduction of pesticide into the environment.

Indian meal moth growth rates on the five processed commodities used in this study varied over a broad range (Fig. 1; Table 2). This commodity effect would also have to be considered when developing strategies that will protect these products during storage. For example, whole wheat flour which supports slow moth growth would require less frequent applications of conventional control procedures to manage a moth infestation than wheat germ which supports more rapid moth growth.

An alternative strategy that would affect the growth rate of moths would be to modify a cereal product, limiting its nutritional value for the Indian meal moth without compromising its utility as a food source for man and domestic animals. Managing moth populations by limiting the

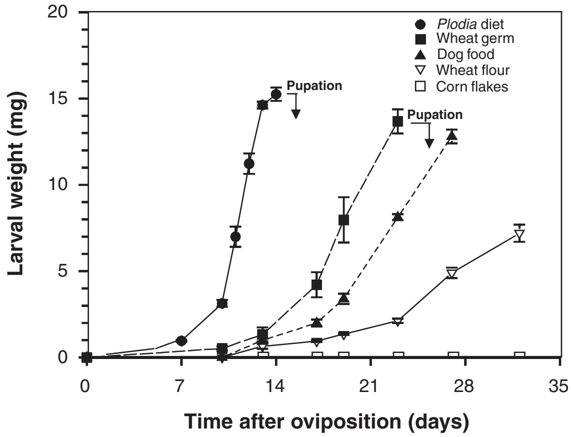

Fig. 1. Growth of Indian meal moth larvae reared on selected commodities to illustrate the range of growth rates on different processed commodities. PD—*Plodia* rearing diet; WG—Kretschmer's wheat germ; DF—Ol' Roy Dinner Rounds dog food; WF—whole wheat flour; CF—Kellogg's corn flakes.

Table 2
Growth parameters ($\pm$SE), defined in Section 2, were determined when a logistic growth curve[a] was fitted to weights of larvae during development on different commodities

Commodity	Growth parameters		
	a	*b*	*c*
Plodia diet	16.1 ± 3.4	11.2 ± 1.0	0.9 ± 0.2
Wheat germ	20.5 ± 3.4	20.1 ± 1.0	2.4 ± 0.2
Dog food	16.7 ± 3.4	23.2 ± 1.0	3.2 ± 0.2

[a]Development on wheat flour was poor, and a logistic curve did not fit the data well and was left out of the analyses that tested the differences among diets. There were differences in growth among the diets ($F = 23.9$; df = 6, 4; $P < 0.01$; using Wilks' λ). Linear contrasts showed that growth was greater on *Plodia* diet than on wheat germ ($F = 138$; df = 3, 2; $P < 0.01$) or on dog food ($F = 346$; df = 3, 2; $P < 0.01$), and was greater on wheat germ than on dog food ($F = 44.5$; df = 3, 2; $P = 0.02$).

availability of an essential nutrient in the processed cereal would provide an attractive alternative to conventional control methods.

3.3. Dietary nutrient requirement

The modification of a food product so as to render it unsuitable for the growth and propagation of insect pests will require a thorough understanding of the insect's nutritional requirements. The first step was to develop a nutritionally defined diet that closely resembled a consumable product in both nutrient and physical characteristics and which would perform as well as standard *Plodia* diet for growing the Indian meal moth.

Fraenkel and Blewett (1946a) pointed out that Indian meal moths could obtain all of their nutrients from the germ of wheat and were unable to use the starch stored in the endosperm for energy. Our results confirmed this observation when we found that wheat germ (Fig. 1) supported larval growth with little or no diminution of final larval size, albeit the growth was appreciably slower than that on standard *Plodia* diet. The rate of growth on whole wheat flour was even slower; probably the assimilation of wheat germ nutrients by the larvae is impeded by the dilution of germ nutrients with non-nutritive kernel components and starch from the endosperm.

Therefore, we were convinced that wheat germ could provide most if not all of the nutrients required for the growth and development of the Indian meal moth and that it could be used as the base component in a much simpler diet. We tried a number of nutritional additives and altered the physical characteristics of wheat germ but were unable to achieve a growth rate comparable to *Plodia* diet (data not shown).

We subsequently found that larval growth on wheat germ could be accelerated by the addition of glycerol. When the glycerol added contributed 30% or 40% to the weight of the wheat germ diet, the larval growth rate was equivalent to or greater than that on *Plodia* diet (Fig. 2; Table 3). However, we observed that the 40% glycerol/wheat germ diet was sticky and that the normal physical activities of the newly hatched larvae were hindered. As a consequence, larval mortality increased from <10% on the 30% glycerol diet to ca. 40% on the 40% glycerol diet.

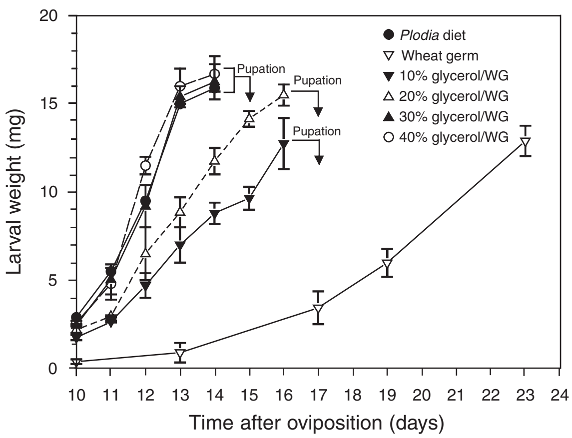

Fig. 2. Growth of Indian meal moth larvae reared on *Plodia* diet (PD), Kretschmer's wheat germ (WG), and several mixtures of wheat germ:glycerol (WG:G percentages, w:w) showing increased growth with increasing levels of glycerol.

Table 3
Growth parameters (±SE), defined in Section 2, were determined when a logistic growth curve[a] was fitted to weights of larvae developing on standard *Plodia* diet or on wheat germ diets with varying amounts of glycerol

Commodity	Growth parameters		
	a	*b*	*c*
Plodia diet	18.5±0.8	11.8±0.1	1.0±0.0
Wheat germ+20% glycerol	17.3±0.8	12.9±0.1	1.4±0.0
Wheat germ+30% glycerol	18.5±0.8	11.9±0.1	0.9±0.0
Wheat germ+40% glycerol	17.6±0.8	11.6±0.1	0.7±0.0

[a]Larval development was poor on wheat germ diets containing no glycerol or 10% glycerol. A logistic curve did not fit these data well, so, they were left out of the analyses to test for differences among diets. There were differences in growth among the diets ($F = 8.75$; df = 9, 10; $P<0.01$; using Wilks' λ). Linear contrasts showed that growth was greater on wheat germ diet containing 40% glycerol than on *Plodia* diet ($F = 7.4$; df = 3, 4; $P = 0.04$), did not differ on wheat germ diet containing 30% glycerol and *Plodia* diet ($F = 2.6$; df = 3, 4; $P = 0.19$), and was greater on *Plodia* diet than on wheat germ diet containing 20% glycerol ($F = 27.4$; df = 3, 4; $P<0.01$). Development did not differ on wheat germ diet containing 30% or 40% glycerol ($F = 1.7$; df = 3, 4; $P = 0.31$).

The stimulation of larval growth with progressive increases in the dietary glycerol levels was surprising; especially, since it was initially added to keep the diet moist by absorbing moisture from the air. The question then became: is the stimulation of growth a specific nutritional effect of glycerol; is it providing an energy source for larval growth; or, is it keeping the dietary water content elevated because of its hygroscopicity?

To clarify this question, we first examined the hypothesis that glycerol provided a readily digestible source of energy for larval growth by being converted to triose phosphate which was subsequently oxidized via glycolysis. If this were true, then any digestible carbohydrate should partially or totally spare the observed glycerol requirement. This idea was tested by substituting glucose for various portions of the glycerol in the wheat germ diet. These tests revealed that glucose could be substituted for about half of the glycerol requirement (Fig. 3; Table 4). Other simple sugars, such as fructose and sucrose, could be substituted for glucose (data not shown). However, not all ingested sugars can be assimilated and metabolized by Indian meal moths (Fraenkel and Blewett, 1946a), in particular, the complex carbohydrates. These results indicated that part of the glycerol requirement was to provide the Indian meal moth with a digestible energy source that entered the glycolytic pathway.

Optimum growth required a minimum of 20% glycerol in the diet when 20% glucose was added to the diet (Fig. 3). The 20% minimum glycerol requirement most likely serves to elevate the moisture content in the diet. This diet, which was optimum for Indian meal moth growth, had a moisture content of ca. 18±1% after equilibration at rearing conditions.

The glycerol- or glycerol/glucose-supplemented wheat germ diets described here meet the criteria of being nutritionally complete diets, whose nutritional composition is largely defined in the US Department of Agriculture Nutrient Database (NDB No. 08084, 2002) and whose nutrient availability is not encumbered by physical limitations. These wheat germ diets provide a starting point for nutritional studies aimed at elucidating the qualitative and quantitative requirements of

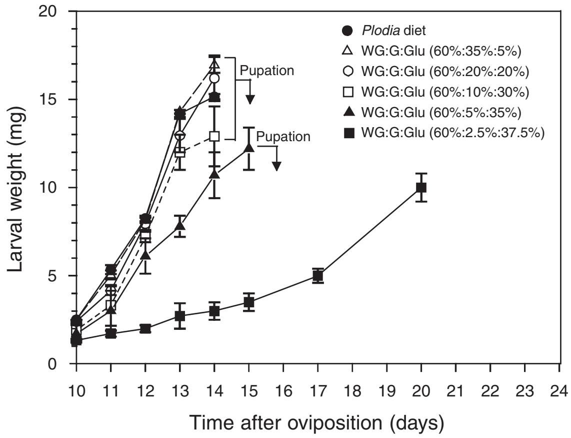

Fig. 3. Growth of Indian meal moth larvae showing that glucose can be substituted for up to one-half the glycerol requirement in supplementing wheat germ as a growth medium for Indian meal moths. Growth on several wheat germ:glycerol:glucose combinations (WG:G:Glu percentages, w:w:w) illustrates this point. Growth on three additional WG:G:Glu mixtures (60%:40%:0%, 60%:30%:10%, 60%:25%:15%, w:w:w) were also tested, but not plotted. These mixtures provided growth rates very similar to that shown for *Plodia* diet.

Table 4
Growth parameters ($\pm$SE), defined in Section 2, were determined when a logistic growth curve[a] was fitted to weights of larvae developing on standard *Plodia* diet or on wheat germ diets containing various mixtures of glycerol and glucose

Commodity	Growth parameters		
	a	*b*	*c*
Plodia diet	17.6 ± 2.8	11.9 ± 0.4	1.0 ± 0.1
Wheat germ + 5% glycerol + 35% glucose	14.7 ± 2.8	12.6 ± 0.4	1.3 ± 0.1
Wheat germ + 10% glycerol + 30% glucose	15.2 ± 2.8	12.0 ± 0.4	0.8 ± 0.1
Wheat germ + 20% glycerol + 20% glucose	24.2 ± 2.8	12.8 ± 0.4	1.2 ± 0.1
Wheat germ + 35% glycerol + 5% glucose	21.6 ± 2.8	12.4 ± 0.4	1.1 ± 0.1

[a]Development on wheat germ containing 2.5% glycerol was poor, and a logistic curve did not fit the data well, so it was left out of the analyses testing for differences among diets. There were differences in growth among the diets ($F = 4.1$; df = 12, 16; $P < 0.01$; using Wilks' λ). Linear contrasts showed that growth on wheat germ diet containing 35% glycerol and *Plodia* diet did not differ ($F = 0.4$; df = 3, 6; $P = 0.76$), growth did not differ on wheat germ diet containing 20% glycerol and *Plodia* diet ($F = 1.2$; df = 3, 6; $P = 0.39$), and was greater on *Plodia* diet than on wheat germ diet containing 10% glycerol ($F = 5.5$; df = 3, 6; $P = 0.04$). Development did not differ on wheat germ diet containing 20% or 35% glycerol ($F = 0.2$; df = 3, 6; $P = 0.88$) or on wheat germ diet containing 10 or 35% glycerol ($F = 4.4$; df = 3, 6; $P = 0.06$). Development did differ on wheat germ diet containing 5% or 35% glycerol ($F = 6.4$; df = 3, 6; $P = 0.03$). Development did not differ on wheat germ diet containing 10 or 20% glycerol ($F = 4.0$; df = 3, 6; $P = 0.07$), but did differ on wheat germ diet containing 5% or 20% glycerol ($F = 7.1$; df = 3, 6; $P = 0.02$). Development also differed on wheat germ diet containing 5% or 10% glycerol ($F = 10$; df = 3, 6; $P < 0.01$).

the Indian meal moth. This knowledge would have applications in predicting susceptibility of cereal products and the management of moth infestations. Furthermore, some processed cereal products of the future could be designed to resist moth infestation by nutrient deletion.

4. Conclusions

Adult females of the Indian meal moth are attracted to a broad range of cereal products for oviposition. The level of infestation was commodity dependent. There were some commodity-specific differences in the level of oviposition that may reflect differences in the levels of attractants or, perhaps, ovipositional stimulants. However, the most important factor affecting the intensity of infestation are commodity-specific differences in the availability of nutrients that support larval growth and development. Nutrient availability depends upon the amounts of nutrients actually consumed and upon physical factors that restrict the ingestion of nutrients.

Investigating the nutritional and physical factors that might be exploited in a strategy to manage Indian meal moth infestation of processed cereals required, as a starting point, a cereal product having a known nutrient composition and having no physical barriers to limit nutrient availability. Wheat germ provides such a commodity when supplemented with glycerol. Wheat germ mixed with 30% glycerol (w:w) supported the growth of Indian meal moths as well as standard *Plodia* diet. This wheat germ diet provides a base for future studies exploring the qualitative and quantitative contributions of specific nutrients that are essential for Indian meal moth infestation of cereal products.

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